12.

The Relationship Between Weight and Body Form in Various Species of Scombroid Fishes.

Sidney Shapiro

The American Museum of Natural History[1]

(Text-figures 1-12).

Organic growth may be defined as increase of the whole organism or any of its systems in weight or in the size of any of its component parts. As thus interpreted growth can be distinguished from differentiation, which represents increase in organization as apart from any measurable increase in the size or weight of an organic system. Growth broken down into its multitude of single processes is difficult to interpret quantitatively, but the direction and amount of growth, considered as a mere quantitative increase of the whole or of its component parts (each of which is the result of a multitude of processes) may be subjected to mathematical analysis. The use of formulas will thus indicate the nature and the types of changes occurring during the life of the organism, although it does not provide an interpretation of the causes of growth.

It has been found that organisms generally show a positive acceleration of growth during early development, after which the velocity shows a negative acceleration. In many investigations the available data cannot take into consideration this time factor, but other growth phenomena may nevertheless be analyzed. Thus the analysis of relative growth indicates how added increments, no matter how small, are being distributed to the component parts of the organism. Relative growth, as distinct from simple growth analysis, does not deal alone with the increase in general size, but rather with the growth and size of any dimension in relation to that of another dimension. These relations determine the form of the organism.

In this paper relative growth methods are used to determine the relation between weight and body form in several fishes generally classed in the suborder Scombroidei. The changes in form during growth are indi-

cated by the analysis of the relative measurements of length, depth and width, as correlated with changes in weight. The mathematical analyses of relative growth during ontogeny exhibit what appear to be fundamental trends and similarities in the type of growth of related species. These developmental likenesses suggest the possible use of such analyses in determining phylogenetic relationships.

Method of Analysis.

The equation $y = bx^k$ has been used by various workers to express the growth of a part (y) relative to that of another part or the remainder of the body (x). The exponent k denotes the constant differential rate of increase of the variables, whereas b, in its simplest connotation, expresses the value of y when x is equal to one. When applied in logarithmic form the equation becomes $\log y = k \log x + \log b$, and the resulting curve is a straight line the value of which is determined by its slope. That a straight line will fit a considerable range of data on differential growth is well substantiated. For example this relation holds for the growth of the large chela of the male fiddler crab, *Uca pugnax*, relative to that of the remainder of the body (Huxley, 1932) ; for the growth of the jaws of certain fishes, *Lepisosteus osseus, Belone* and *Hemirhamphus far,* relative to that of the remainder of the body (Needham, 1935) ; and that of the abdomen of the pea-crab, *Pinnotheres pisum,* relative to that of the carapace (Williams and Needham, 1938).

This empirical equation adequately states the ontogenetic change in the relative size of the parts or organs under consideration, despite the fact that the exponential value k lacks dimensions and is a "pure number." Growth is basically dependent on the multiplication of living substance, but the increase in each part of the organism occurs at a specific rate. As growth progresses there

occur various readjustments and changes in proportions, depending on the relative growth rates. These changes can be readily analyzed by the logarithmic method.

The use of the equation $y=bx^k$ has been extended for a study of other relationships. A specific instance, where weight (y) has been assumed to be proportionate to the cube of the length $(k=3)$, has been employed by Crozier and Hecht (1913), Hecht (1916), and Van Oosten (1928) to study the relationship of weight to length in fishes. Keys (1928) and Marshall, Nicholls and Orr (1937) have also studied this relationship of weight to length and have demonstrated the applicability of the equation when both b and k are determined empirically.

The use of different terms by various workers has confused the literature on relative growth. Since the equation expresses the growth of a part relative to the whole or another part, k was first termed the constant differential growth ratio (Huxley, 1924). In a revision of terminology, Huxley and Tessier (1936) preferred to designate k as the equilibrium constant. The value of b, the size of the organ or part when the standard is 1, has been referred to as the initial growth index. It is a theoretical number, representing the intercept value of the regression line, and does not actually indicate the weight, depth or width of the fish having a length of 1, but it does define the proportionate relations of the fish, beginning at the length at which the straight line relations for relative growth are established. The growth ratio (k) indicates the relative sizes of the increments of each variable during growth and is thus indicative of the proportional changes in the dimensions. When one part grows at the same rate as another part of the body $(k=1)$, the relative increases in growth of the two variables are equal and the proportions remain undisturbed. Pezard (1918) denotes this specific condition of growth "isogonic" and this term was adopted by early workers. Other terminology used to designate such growth has been "harmonic growth" (Champy, 1929) and "isometry" (Huxley and Tessier, 1936). If the rates are unequal, growth is said to be heterogonic (disharmonic, or allometric) in a positive or negative direction. When the dependent variable (y) increases at a rate greater than that of the part or organ (x) to which it is being compared, the allometry is positive. If the constant differential growth ratio is less than unity the relationship is such that the dependent variable shows negative allometry.

A number of difficulties have been pointed out by various workers in the use of the logarithmic representation. Gray (1929) explains the obvious effect upon apparent variation that logarithmic representation necessarily introduces. With the transformation to logarithmic values the diameter of a dot on the graph may be greater than the error of the measurement of the variable, since the scale of the graph becomes proportionally smaller with the larger measurements. Thus when the dots are extremely close together they may fit the line of the curve and yet conceal small but significant variations. For this reason, in a study of allometric growth, statistical methods, rather than graphical procedures, should be used for the determination of the constants.

Another difficulty arises in the grouping of the data. The use of averages will minimize the natural variation of the larger specimens and overemphasize that of the smaller specimens. Therefore in grouping the data for this study the actual data were first converted to their logarithmic values and then grouped according to the increasing geometric scale. In this manner the variation for the larger specimens was given the same value as that for the smaller specimens.

The value of the growth constants was determined by the use of the product moment method. In the analysis of such data most workers have made use of only one regression line—that of the dependent variable in relation to the independent variable. Statistically this equation is known as the regression of y upon x. Because of the irregularities in variation shown by anything less than an infinite number of specimens, a single regression line will not fit a series of data, especially those collected under different environmental conditions. Therefore another regression line of the best value for the independent variable in relation to the dependent variable (the regression of x upon y) has been determined. The regression value for x upon y has been converted to its reciprocal value so as to be expressed in the same terms as the regression of y upon x. Two such regression lines make interpretation difficult but the mean regression line, determined from the two, will give a simple average value for all the available data. These mean regression lines are conveniently comparable. Each such line contains a theoretical k value and since the two k values for each regression are very similar (compare k_{yx} and k_{xy} in Tables 2, 3), the value of k for the mean regression line k_{av} must be near its true value.

METHOD OF WEIGHING AND MEASURING.

Because of considerable postmortem changes, measurements and weights were taken as soon as possible after the fish were out of the water. Tests made of weight changes due to water loss or gain during the brief intervening period showed negligible differences. Some of the fish were kept alive until weighed and measured. Weight for the smallest fish was determined

TABLE 1.   VALUES OF *n* AND *a* FOR THE PARTITION OF GROWTH INCREMENTS OF BODY WEIGHT RELATIVE TO THE STANDARD BODY LENGTH.

The exponent n_{yx} gives the values for the regression line of weight upon length; n_{xy} is the value for length increase upon weight, but still expressed in terms of the standard length, and *n* is the geometric mean value for n_{yx} and n_{xy}. The species for the various families are arranged in descending order for the value of *a*. The range of the data for the weight in grams and the length in millimeters is given for each species.

SPECIES	n_{yx}	n_{xy}*	n	a	RANGE WEIGHT IN GRAMS	RANGE LENGTH IN MM.
Pomatomidae						
Pomatomus saltatrix	2.962	3.001	2.98	.0000229	65.0 — 1040	145— 363
Carangidae						
Caranx hippos	2.779	2.829	2.80	.0000858	51.0 — 738	116— 312
Vomer sctapinnis	2.823	2.849	2.84	.0000648	5.4 — 158	55— 180
Caranx crysos	2.838	2.892	2.87	.0000562	22.6 — 201	96— 203
Selene vomer	2.957	2.989	2.97	.0000483	1.3 — 79	30— 122
Trachinotus falcatus	3.082	3.107	3.09	.0000350	.06— 3	11— 39
Trachinotus carolinus	3.044	3.054	3.05	.0000264	.07— 773	14— 304
Scombridae						
Scomberomorus maculatus	2.825	2.849	2.84	.0000288	57.0 — 1730	167— 552
Trichiuridae						
Trichiurus lepturus	3.352	3.374	3.36	.0000000674	8.8 — 396	263— 810
Istiophoridae						
Makaira nigricans ampla	3.313	3.679	3.49	.000000161	41220.0 —243260	1950—3040
Makaira nigricans marlina	3.500	3.582	3.54	.000000118	47560.0 —369200	1950—3290

* The values given in this column are the reciprocal values of n_{xy}. They express the increase of length upon weight in terms of the standard length.

by a chemical balance, for the medium-sized ones by a triple balance scale, and for the largest by a spring scale. Standard length is here expressed as the distance from the tip of the snout to the vertical of the minimum depth of the caudal peduncle (that is, to approximately opposite the front edge of the hypural plate). For each species the depth was taken at the same point on each specimen, yielding the maximum measurement; correction was made to compensate for distension due to stomach contents. Width was taken where greatest.

THE LENGTH-WEIGHT RELATIONSHIP.

Early work on the relationship of weight to length resulted in the formulation of the cube law by Spencer (1871). Hecht (1916), Van Oosten (1928) and others further applied this principle to the growth of fishes. Most of these authors assumed that there exists, in fish, a long-continued period with no change in external proportions (or in specific gravity) and consequently that, in the equation $y=bx^k$, *k* is equal to 3. These workers were thus necessarily concerned only with the variation of the coefficient *b*. If the cube law holds for the greater portion of the fish's life, it would necessarily mean that the final form is established early and that enlargement in each dimension is a linear function of length. Secondly the density must remain unchanged in order to avoid allometric growth.

There are theoretical limitations to the simple cubic function, since the direct relationship is between length and volume, rather than between length and mass. Mass is proportional to volume only in a body of constant density. Hence in expressing the weight of a complex heterogeneous body in

Table 2. Values of k and b for the Partition of Increments of Body Depth Relative to the Standard Body Length.

The exponent k_{yx} denotes the value for the regression line of depth upon length; k_{xy} is the value for length increase upon depth, but still expressed in terms of the standard length, and k is the geometric mean value for k_{yx} and k_{xy}. The species of the various families are arranged in descending order for the value of b. The range of the data for depth and length, both in millimeters, is given for each species.

Species	k_{yx}	k_{xy}*	k	b	Range in Size Depth	Range in Size Length
Pomatomidae						
Pomatomus saltatrix	0.865	0.903	0.88	0.529	41.0—102	145— 363
Carangidae						
Vomer setapinnis	0.744	0.764	0.75	1.970	39.0—110	55— 180
Selene vomer	0.914	0.925	0.92	1.140	28.0— 94	30— 122
Caranx hippos	0.794	0.821	0.81	1.060	49.0—102	116— 312
Caranx crysos	0.870	0.927	0.90	0.581	34.0— 66	96— 203
Trachinotus falcatus	1.235	1.257	1.25	0.259	5.4— 25	11— 39
Trachinotus carolinus	1.127	1.131	1.13	0.251	4.6—124	14— 304
Scombridae						
Scomberomorus maculatus	0.860	0.884	0.87	0.414	40.0—109	167— 552
Trichiuridae						
Trichiurus lepturus	1.166	1.187	1.18	0.022	15.3— 57	263— 810
Istiophoridae						
Makaira nigricans marlina	1.175	1.298	1.24	0.033	384.0—760	1950—3290
Makaira nigricans ampla	1.213	1.433	1.32	0.016	330.0—670	1950—3040

* These values are the reciprocals of the regression values for increase of length (x) upon weight (y). They express the increase of x on y in terms of the standard length.

terms of length the equation would hardly be expected to take the form of a cubic parabola although it may approximate one. The specific gravity of the watery environment of most fishes remains fairly constant, and as free-swimming fishes like the Scombroidei are in close hydrostatic equilibrium with their environment they must maintain a constant specific gravity. If there are uncompensated changes in the specific gravity of the fish (due to the altered density of various parts of the organism, such as bone or adipose tissue, or altered proportions of these parts), and if the specific gravity remains in equilibrium with the surroundings, some change in body form would be necessitated. Therefore changes in the dimensions of the body may compensate for a tendency toward change in density and thus maintain the organism at a specific gravity equal to that of the surrounding medium.

It is now commonly recognized, as the result of numerous researches, that the cube relationship between weight and length is only an approximation, and at times is not even closely realized. The application of the allometric formula, $y=bx^k$, for a study of the relationship of weight to length has been applied successfully by various workers to the post-metamorphic period of fish development. Keys (1928) demonstrated that the weight of the killifish (*Fundulus parvipinnis*), the European herring (*Clupea haren-*

gus), and the California sardine increases at a rate greater than the cube of the length and less than the fourth power of the length. In an analysis of the growth of the blue marlin, Shapiro (1938) demonstrated greater increments of weight relative to increasing increments of length ($k>3.00$) and that form change was taking place during the post-metamorphic growth. By means of statistical methods Keys was able to show that variations in both k and b denote change of form. Therefore, if we are to study adequately the implications of weight in relation to form the equation should be determined empirically.

The formula $W=aL^{n^2}$ implies the same conditions that have been expressed for the growth of a part relative to another part or the remainder of the body. Weight (W) and length (L) are the variables under consideration; the exponent n indicates the relative increases of these variables during the growth of the fish. The coefficient a is indicative of the units of measurement used (Keys, 1928) and also denotes the value of the weight when the length is mathematically equal to 1. It thus serves as an index of the initial relationship existing between the two variables at the point where both are reduced to a single theoretical unit. It is true that a will fluctuate seasonally with-

[2] These symbols are used for the allometry formula of weight in relation to length as distinguishable from the general formula, $y=bx^k$, to denote relationships of dimensions, i.e., width and depth.

TABLE 3.   VALUES OF k AND b FOR THE PARTITION OF INCREMENTS OF BODY WIDTH RELATIVE TO THE STANDARD BODY LENGTH.

The exponent k_{yx} denotes the value for the regression line of width upon length, k_{xy} is the value for length increase upon width, but still expressed in terms of the standard length, and k is the geometric mean value for k_{yx} and k_{xy}. The species are arranged in descending order, within each family, for the value of b. The range of data for width and length, both in millimeters, is given for each species.

SPECIES	k_{yx}	k_{xy}*	k	b	RANGE IN SIZE DEPTH	LENGTH
Pomatomidae						
Pomatomus saltatrix	1.170	1.236	1.20	0.040	16.0— 49	145— 363
Carangidae						
Caranx crysos	1.014	1.107	1.06	0.109	13.0— 57	96— 203
Caranx hippos	1.091	1.145	1.12	0.086	18.0— 49	116— 312
Selene vomer	1.065	1.079	1.07	0.086	4.1— 15	30— 122
Vomer setapinnis	1.107	1.131	1.12	0.057	5.3— 20	55— 180
Trachinotus carolinus	1.034	1.042	1.04	0.012	3.1— 40	22— 304
Scombridae						
Scomberomorus maculatus	1.075	1.114	1.10	0.057	16.0— 55	167— 552
Trichiuridae						
Trichiurus lepturus	1.318	1.344	1.33	0.0025	4.2— 19	263— 810
Istiophoridae						
Makaira nigricans marlina	1.313	1.533	1.42	0.0040	190.0—425	1950—3290
Makaira nigricans ampla	1.230	1.725	1.46	0.0027	165.0—320	1950—3040

* These values are the reciprocals of the regression values for increase of length (x) upon width (y). They express the increase of x on y in terms of the standard length.

in the limits of variation and consequently some investigators (mostly those who have worked with the cube law) have used this coefficient as a measure of the condition of the fish or the state of sexual development. We prefer to use it not as a measure of fluctuating heaviness but of relative bulk, specific for each type of fish.

The empirical determination of the relationship between weight and length shows that each species maintains its specific growth ratio. The range of the exponent n is from 2.80 in *Caranx hippos* to 3.54 in *Marlina nigricans ampla* (Table 1, Text-figs. 1-4)[3]. Those species with a value below 3.00 are maintaining a negatively allometric increase of weight for each unit increase of the length. Thus, among the carangids, *Caranx hippos* and *C. crysos* (Text-fig. 1) and *Selene vomer*[4] and *Vomer setapinnis* (Text-fig. 2) become relatively lighter with increase in length. Among the species studied of closely allied families, *Scomberomorus maculatus* shows a similar condition.

The weight increases exactly as the cube of the length only when an isometric relation between these variables is maintained. This is a special case of growth similar to

the previously-explained isometric condition where linear dimensions were considered, but here growth would proceed either isometrically along all three geometric axes, or the allometric growth along different axes would be exactly compensating. The only species approximately showing this special isometric length-weight relation is the bluefish (*Pomatomus saltatrix*). For this species the value of n is 2.98 but the regression weight on length shows a value of 2.962 and of length on weight 3.001 (Table 1). If we interpret this almost ideal weight—cube–length relationship on the basis of no change in form (as the cube law would demand), *P. saltatrix* should maintain constancy of body form during growth. The linear dimensions of depth and width, however, show no approach to the condition of unchanging proportions. The constant differential partition of growth increments in relation to the length is 0.88 for the depth (Table 2) and 1.20 for the width (Table 3). Since these exponential values deviate about equally from the value (1.00) for isometric growth they are approximately compensating, and the weight increases about as the cubic function of the length.

The remaining species studied show a positive allometric increase of weight in terms of length. *Trachinotus carolinus* and *T. falcatus* show a slight tendency to become heavier with increase in length (Text-fig. 3, Table 1) but *Trichiurus lepturus* and

[3] The growth constants for *Caranx crysos* have been determined only for those fish up to 203 mm. in standard length. The specimens above this size depart significantly from the curve in a more positive direction. Whether this deviation is due to a change in the growth rate at this point or to an insufficiency of accurate measurements cannot be determined as yet.

[4] *Selene vomer* is currently recognized as being synonymous with *Argyreiosus vomer*.
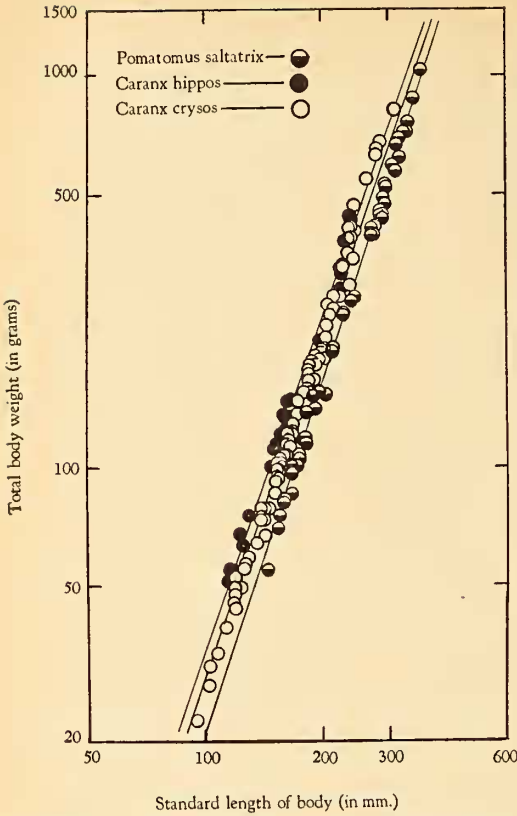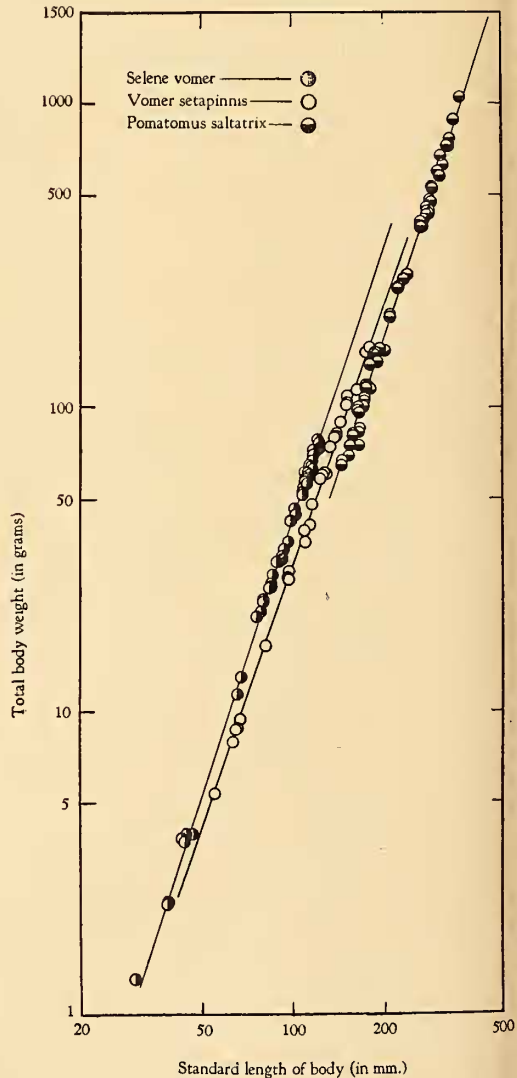
TEXT-FIG. 1. Increase of total body weight with standard body length; logarithmic plotting for both weight and length.

may be growing at different rates, since positive exponential values in some sections of the body may just compensate negative values in other parts. The results obtained with the remaining species indicate that unmeasured proportions of the body change with age, for the sum of the exponents of the linear dimensions often does not closely approximate the value of n (Table 4).

A comparison of the initial growth index (a) with the size attained by the various species indicates that the larger fish tend to show a smaller coefficient of bulkiness (Table 1). At the inception of the post-metamorphic straight line relation *Trichiurus lepturus* ($a=0.0000000674$) and *Makaira nigricans ampla* ($a=0.000000161$) and

both subspecies of *Makaira* maintain a high positive allometry (Text-fig. 4, Table 1).

In studies of length-weight relations the measurement of maximum length, depth and width have been uncritically accepted as representing precisely the form of the fish throughout life. Changes in shape, however, may take place in portions of the body which have not been measured, for instance the head and peduncular regions. In an analysis of numerous dimensions of *Makaira nigricans ampla* (Shapiro, 1938), the gradients for different parts of the fish were shown to differ considerably, the tendency being for the exponential values to be more intense posteriorly and less so anteriorly. Only if the shape of all sagittal and all frontal sections remained constant, would the maximum depth and width measurements accurately represent the form. In that case the sum of the exponential values for the three axes should equal the value of n in the length–weight formula. *Selene vomer* and *Vomer setapinnis* are the only species in this study that maintain such a condition (Table 4), although the possibility still exists that various sections of their body too

TEXT-FIG. 2. Total body weight against standard length; logarithmic plotting both ways.

TABLE 4. SUM OF EXPONENTS FOR LINEAR DIMENSIONS COMPARED WITH EXPONENT FOR LENGTH-WEIGHT RELATIONSHIP.

If the three geometric axes of length, depth and width adequately represent the form of the body, the sum of their exponential values should equal the value of n for the length-weight relation. If the sum of the k values of these axes does not closely approximate the value of n, changes in shape of other portions of the body are taking place and the maximum measurements of length, depth and width are not truly representative of the form of the body.

	VALUE OF k FOR			SUM, 1+2+3	VALUE OF n
	(1) LENGTH	(2) DEPTH	(3) WIDTH		
Pomatomus saltatrix	1.00	0.88	1.20	3.08	2.98
Caranx hippos	1.00	0.81	1.12	2.93	2.80
Caranx crysos	1.00	0.90	1.06	2.96	2.87
Vomer setapinnis	1.00	0.75	1.12	2.87	2.84
Selene vomer	1.00	0.92	1.07	2.99	2.97
Trachinotus carolinus	1.00	1.13	1.04	3.17	3.05
Scomberomorus maculatus	1.00	0.87	1.10	2.97	2.84
Trichiurus lepturus	1.00	1.18	1.33	3.51	3.36
Makaira nigricans ampla	1.00	1.32	1.46	3.78	3.49
Makaira nigricans marlina	1.00	1.24	1.42	3.66	3.54

M. n. marlina ($a = 0.000000118$) have decidedly smaller bulk per unit length than do the deeper-bodied and shorter forms of the carangids, such as *Vomer setapinnis* ($a = 0.0000648$) and *Selene vomer* ($a = 0.0000483$). In its a value of 0.0000288, *Scomberomorus maculatus* approaches slightly the condition of the specialized fusiform Istiophoridae and the elongate Trichiuridae. The value of a for *Trachinotus carolinus* (0.0000264) and *T. falcatus* (0.0000350) is low as compared with the other carangids. It is similar to the value for a central scombrid form like *S. maculatus*. Thus, for unit length, the longer fish, at the point where differentiation has been completed and post-metamorphic growth is beginning to follow the straight line relation, show a low weight coefficient as compared with the high value for the deep-bodied forms.

If a is accepted as an indicator of the type of body form, the eleven species of fish can be arranged in a series grading from the deep-bodied to the elongate type. The use of the initial growth index for this purpose disregards the changes in body form that take place during post-metamorphic growth. The value of a is high for the deep-bodied compressed forms such as *Selene vomer* and *Vomer setapinnis*. Their greater relative bulkiness at the beginning of the post-metamorphic growth period seems to be directly correlated with their extreme depth and shortness of body. The moderately elongated fusiform type, represented by the mackerel, bluefish and pompano (*Trachinotus carolinus*), show central values of a (smaller bulkiness per unit length than in the deep-bodied forms). The most specialized, elongated types, represented by the cutlass fish (*Trichiurus lepturus*), give the low values at the other extreme of the series. In this species the theoretical bulk per unit length at the beginning of the post-metamorphic period is incredibly small. It should be pointed out that the standard length of the marlins was determined with the enormous bill included. The value of a would be somewhat higher if the sword were discounted and would place them closer to the category of the fusiform mackeral type.
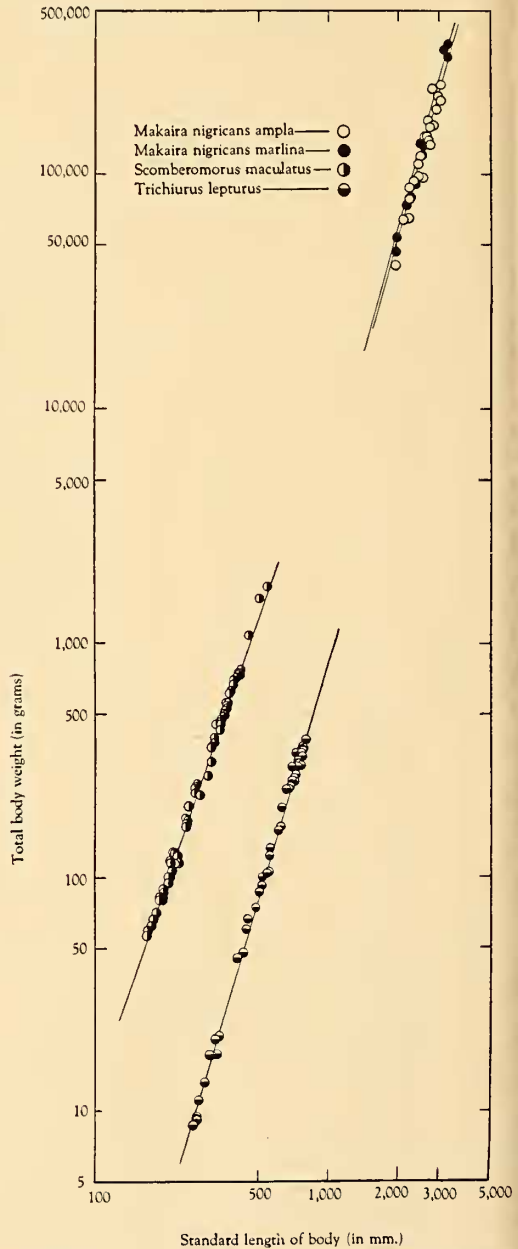
That there is a relationship between a and n can be shown by plotting these values for the different species on semi-log paper (Text-fig. 5). The general tendency is such that n increases in arithmetical progression as a decreases in geometrical progression, thus conforming to an exponential function wherein log a shows a definite rate of decrease in terms of increase of n. Hersh (1931, 1934) found that, in the relative growth of genetic mutants of *Drosophila* and in the evolutionary relative growth of the Titanotheres, this same exponential relationship holds true. Lumer (1939) also obtained an inverse relationship between the constants for the radius-humerus and leg-arm relations in the Pongidae. Thus, if the value for a suggests a slim fish per unit length at the termination of its larval growth, its weight increase, relative to the length, for the post-metamorphic period is correspondingly greater (compare values for a and n in Table 1). *Makaira nigricans ampla*, *M. n. marlina* and *Trichiurus lepturus*, with the low a values of a slim fish, show a steeper gradient for the distribution of weight as the fish increases in length, whereas the reverse is true of the deeper-bodied fish. The trend of a in relation to n for the various families has been indicated by the broken lines on Text-fig. 5. It may signify that the exponential relationship is distinctive for each family and therefore of some value in determining phylogenetic trends.
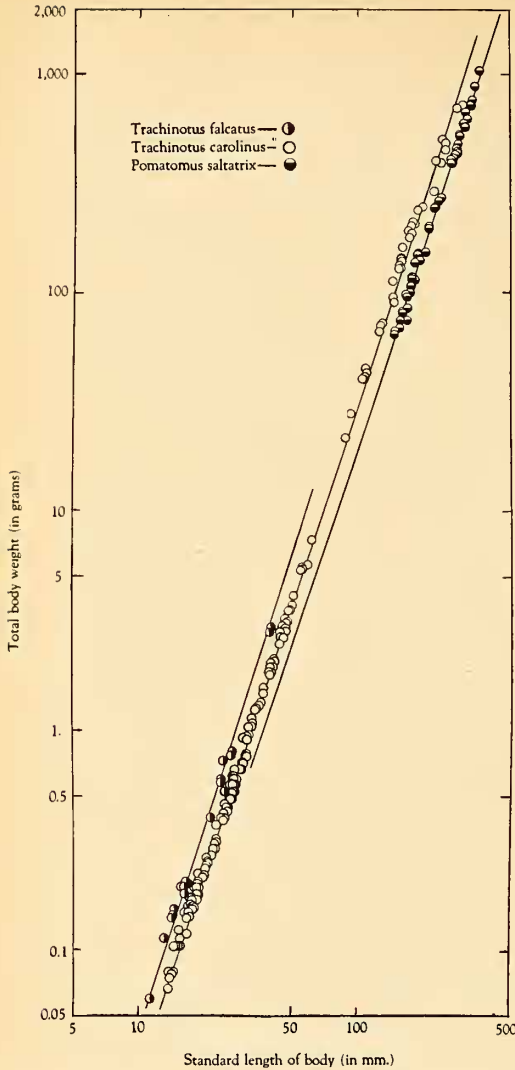
TEXT-FIG. 3. Increase of body weight with increase of standard body length; logarithmic plotting both ways.
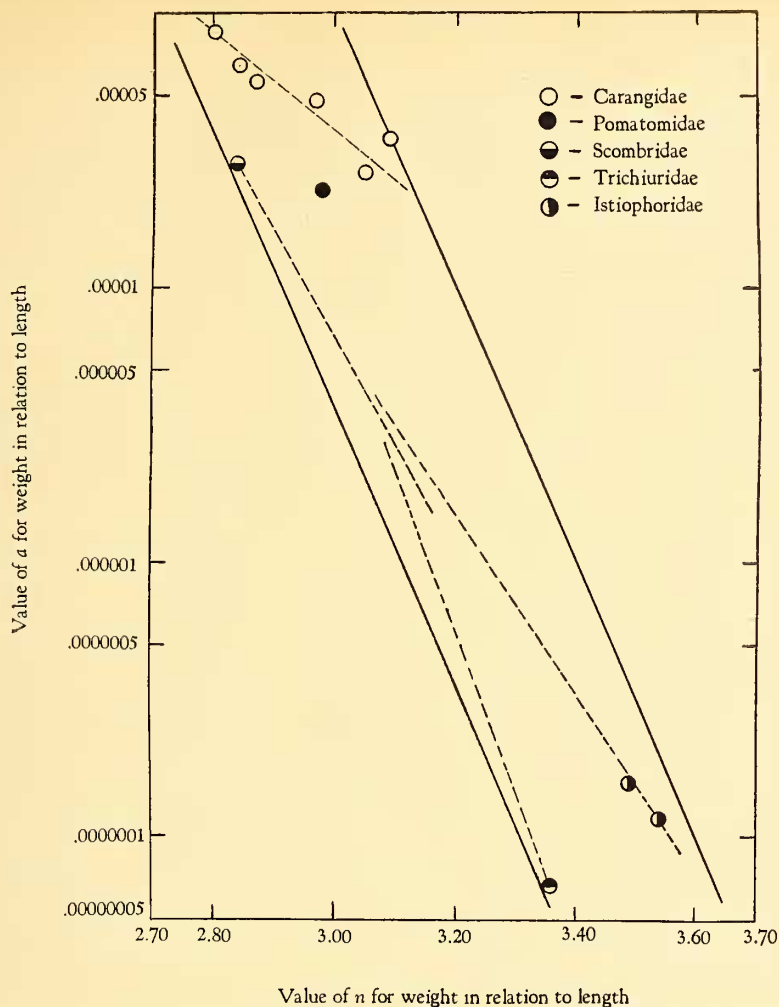
hippos relatively heavier than *C. crysos* (refer to Text-figs. 1 and 3). There is a distinct tendency for convergence between the species of *Caranx* (eventually the index of weight to length becomes the same for both), but for divergence between the species of *Trachinotus*. The relative growth rates for the post-metamorphic period appear to be broadly similar for closely re-

TEXT-FIG. 4. Total body weight relative to standard body length; logarithmic plotting both ways.

The values of n (Table 1) indicate that closely allied members of the various families tend to have similar coefficients of growth partition. The species *Caranx hippos* and *C. crysos* have values of 2.80 and 2.87 respectively, *Trachinotus carolinus* 3.05 and *T. falcatus* 3.09, and *Makaira nigricans ampla* 3.49 and *M. n. marlina* 3.54. Although similar within each genus, the species of *Caranx* and of *Trachinotus* show no overlapping of the regression lines for n_{yx} and n_{xy} (Table 1). Therefore the species can be separated by their constant differential growth ratio, as well as by differences in weight at the same length. *T. falcatus* is relatively heavier than *T. carolinus* and *C.*

TEXT-FIG. 5. Values of *a* for weight in relation to length plotted logarithmically against the growth coefficients (*n*) for weight relative to length; *n* plotted on an arithmetic scale.

lated species, but specific differences are maintained.

DEPTH AND WIDTH AS A MEASURE OF BODY FORM.

For the body measurements (depth and width in relation to length) the relationships are linear and have been expressed either by the equation $y = a + bx$ or by the geometric form $y = bx^k$. Which equation is more applicable to the data? Meek (1905) and Hecht (1916) used the first equation, for they maintained that, if the lines for the growth of the dimensions of the body converge to zero when plotted in relation to length, the equation becomes $y = bx$. This isometry equation is therefore applicable when the growth coefficient is close to 1 and will fit the data as well as the allometry formula. But what of the instances when the data does not show the specific case of isometry? The first equation ignores the difference of *k* from one, whereas the second equation ignores the difference of *a* from zero. If the growth involved is geometric the factor *a* is small and no valid error results from ignoring it. Simpson and Roe (1939, p. 370) show that the allometry formula fits the facts better than does the isometry formula when growth is markedly allometric, as it often is.

The values for the constant differential partition of depth in relation to length show negative allometry for some species, and definitely positive allometry for others. Among the Carangidae the values for the
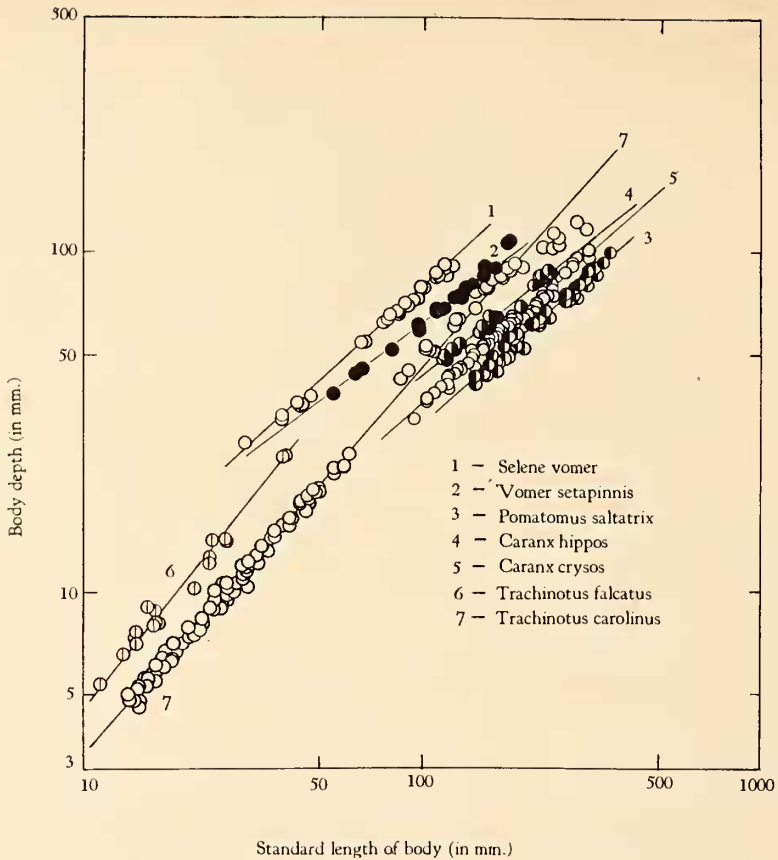
TEXT-FIG. 6. Relative increase of depth in terms of the standard length for the Pomatomidae and the Carangidae. Scale both ways in logarithmic increase.

partition of the growth increments range from 0.75 for *Vomer setapinnis* to 1.25 for *Trachinotus falcatus* (Text-fig. 6). Thus in *V. setapinnis* the body is becoming slenderer to the extent that each unit increase of depth is 0.75 of each unit increase in length. The reverse is true for the positively allometric *T. falcatus*, which becomes relatively deeper as it grows longer. None of the carangids show an ideal isometric condition. *Scomberomorus maculatus* and the allied Trichiuridae and Istiophoridae show relations similar to those exhibited by the Carangidae (Table 2, Text-fig. 7). *S. maculatus*, with a value of 0.87 for k, grows increasingly slender, whereas *Trichiurus lepturus* ($k = 1.18$) and *Makaira nigricans ampla* ($k = 1.32$) and *M. n. marlina* ($k = 1.24$) shows definitely positive allometric increases in depth.

The significance of such trends may be correlated with the total size that the fish attain and with the value of the gradient for the deposition of weight. According to Glaser (1938) form is of prime importance

and therefore the usefulness of an organ and the adaptiveness of an organism to its environment are to some degree functions of the weight. Changing proportions place upon the organism the necessity of coping with the environment in a constantly differing way. If the environment does not directly affect the direction of growth of the various dimensions, selection in the course of evolutionary change must adjust these factors to maintain an efficient mechanism for the locomotion of the fish as its body weight increases. With an increase in the relative bulk of the fish (i.e., when $n > 3.00$) there must be an increase in one or more of the transverse body dimensions. Of the species studied, all those which become relatively heavier with increased length, namely *Trachinotus carolinus*, *T. falcatus*, *Trichiurus lepturus*, *Makaira nigricans ampla* and *M. n. marlina*, also become relatively deeper (compare values of n in Table 1 with values of k in Table 2).

All species studied show positive allometry for the relationship of width to length (Table
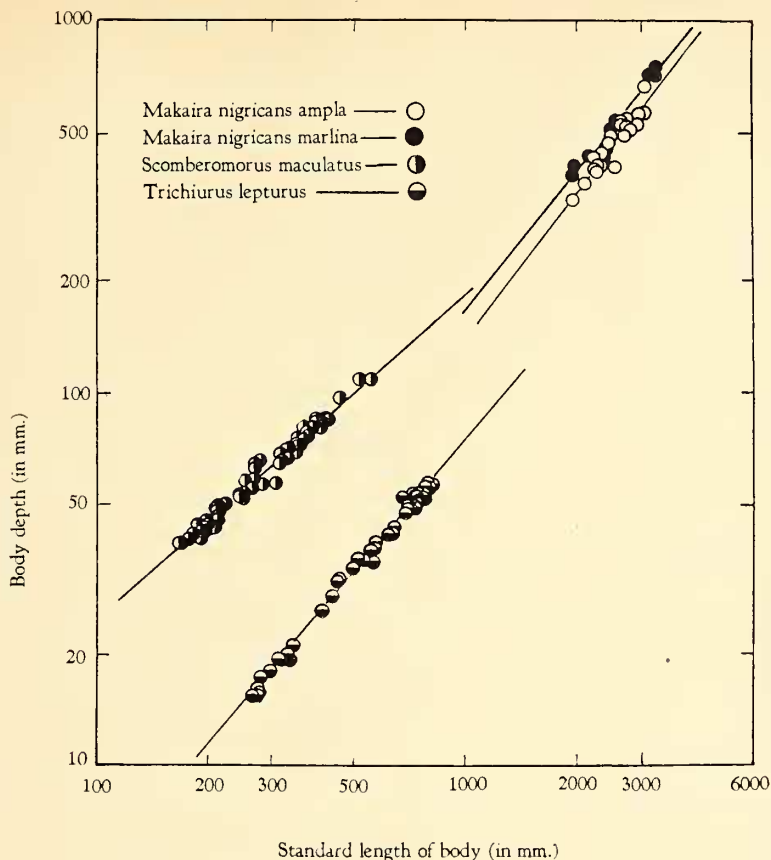
TEXT-FIG. 7. Body depth relative to body length for the Scombridae and the allied Trichiuridae and Istiophoridae. Logarithmic plotting both ways.

3). They grow in such a manner that the width increases at a proportionally greater rate than the length (Text-figs. 8-11). Thus fishes (*Scomberomorus, Selene, Vomer,* or *Caranx*) which become relatively lighter ($n < 3.00$) must do so through a relative decrease in depth.
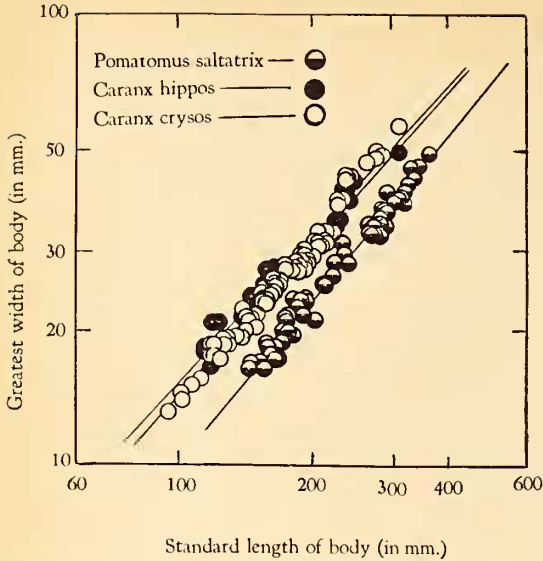
In all the genera, with the exception of *Trachinotus*[5], the differential growth in width proceeds more rapidly than the growth in depth (compare values of k in Tables 2 and 3), even in *Trichiurus* and *Makaira,* which show a positive allometric increase in each dimension. The change to a heavier fish proceeds more rapidly along the transverse than along the vertical axis (except in *Trachinotus*). In *Trachinotus carolinus* both depth and width become proportionally greater than length, but the depth maintains a steeper gradient of growth than does the width.

The species studied also show significant

resemblances and differences in the value of the coefficient b (Tables 2 and 3). In general this value is lower in the more specialized forms (*Makaira nigricans ampla, M. n. marlina, Trichiurus lepturus* and *Trachinotus carolinus*) than in the more deep-bodied, compressed species. For example, in *T. lepturus* $b = 0.022$ for depth and 0.0025 for width, whereas in *Vomer setapinnis* $b = 1.97$ for depth and 0.057 for width.

In general there is a negative correlation between the values of the coefficients a and b on the one hand and the values of the exponents n and k on the other hand (Tables 1-3). This correlation holds particularly well when the comparison is made between species of the Carangidae and between those referred to the Scombridae, Trichiuridae and Istiophoridae. In biological terms, the species which are the deeper and the wider initially become relatively slenderer and thinner with age, and *vice versa.* In the species studied, therefore, the body form is the more diverse in the young stages, and what might be called an interspecific regulation

[5]The value for k for the relation of width to length in *T. falcatus* could not be determined because of the large error involved in measuring the small fish which alone were obtainable.

TEXT-FIG. 8. Body width relative to standard body length plotted logarithmically both ways.

in growth tends to mold the adults into a more uniform and conventional fish-form.

RELATIVE GROWTH IN RELATION TO PHYLOGENY AND SYSTEMATICS.

The growth intensity of the body as a whole is being distributed according to an orderly system of growth gradients (Thompson, 1917; Huxley, 1932). Each species of scombriform fish here analyzed has been shown to possess an individual and specific pattern of growth, and the relative changes in depth and width have indicated certain similarities for closely related species. It is our purpose to evaluate these specific growth gradients and determine whether or not there is an interspecific trend into which these individual growth gradients will fall.

Such allometric growth analysis has been used by other workers to indicate trends in evolutionary growth-partition. Hersh (1934) has pointed out that evolution in the Titanotheres proceeds by constant change in the proportion of dimensions as the size of the species increases. In some skull relations, all the species show a uniform relation between b and k and a single straight line curve is obtained, while for other relations a set of curves, each distinct for a genus, results. The differences within any curve are apparently due only to differences in size that the species within a group curve attain. Each curve is based entirely upon measurements of adult individuals and the ontogenetic growth constants are not considered. Similar results have been obtained with the horses. All fossil and modern horses show a distinct group trend with reference to the muzzle length-total skull length relation (Robb, 1935a), while for the relation between the length of the splints and the length of the cannon bone, two distinct bands are produced, one for the four-toed and three-toed horses and the other for the one-toed forms (Robb, 1936). The horse is characterized by a progressive increase in body size from the Eocene on and, therefore, these curves represent stages in geological time. In the horses the ontogenetic curves are of the same value as the evolutionary group curve (Robb, 1935b). Lumer (1940) has shown that various tribes of 'dogs may be separated upon their different allometric trends, but here again, as in Hersh's study, no indication of the ontogenetic development is given.

When orthogenetic trends are not present the group curve will represent merely averages of the ontogenetic curves. In this study of scombriform fishes, species within the same genus show distinctly different growth constants. Evolutionary relative growth (which makes use solely of adult measurements) should, in the strict sense, be applied only to groups where the larger species recapitulate in their development the body proportions of the adult stages of smaller species.

The scombriform fishes continue growing throughout life (with body proportions constantly changing) and no definite mature stage can be selected for an evolutionary comparison. Furthermore there is evidence that this group has numerous phyletic lines. Therefore, in order to set up a phyletic system for these fishes (or for any group that does not show an orthogenetic trend) on the basis of relative growth data, the ontogenetic growth constants must be considered. There ought to exist among the members of a genus, or of a higher group, similar trends in these growth constants. That such trends exist in the scombriform fishes is indicated below.

If the values of k for the growth partition of width and depth (each relative to length) are plotted against each other (Text-fig. 12), it is possible to observe the interspecific trends of the gradients. Since these trends exist, it becomes important to determine whether the ontogenetic change in proportions, characteristic of each species, is a clue to their phylogenetic relationships. Some evidence favorable to this view has been obtained. The lines obtained by the changes in the intensity of the growth constants divide the Scombroidei into two major groups—on one hand the Scombridae with the allied Trichiuridae and Istiophoridae, and on the other the Carangidae (this point is further discussed below). In the scombroids there is a general tendency from the central mackerel type in the direction of
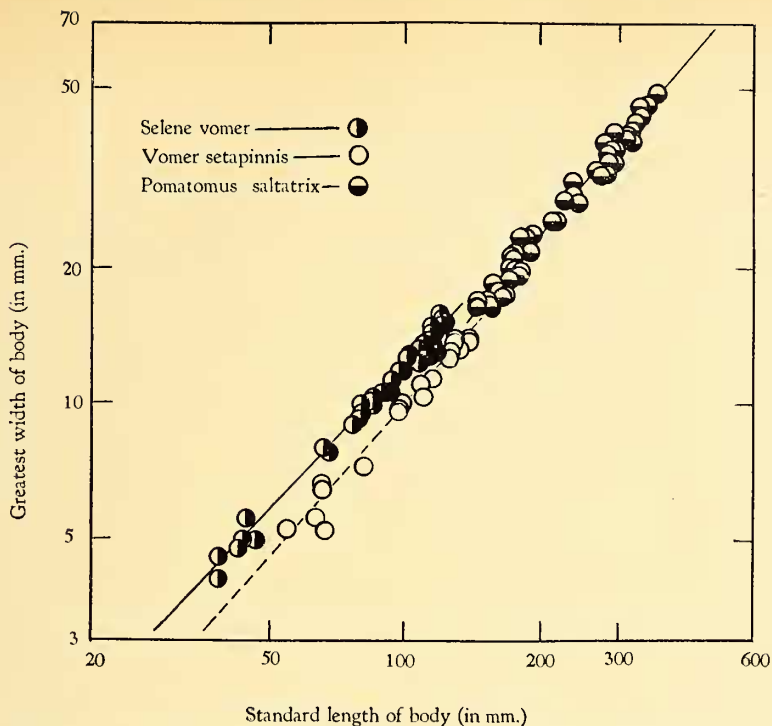
TEXT-FIG. 9. Increase of width relative to length; logarithmic plotting both ways.
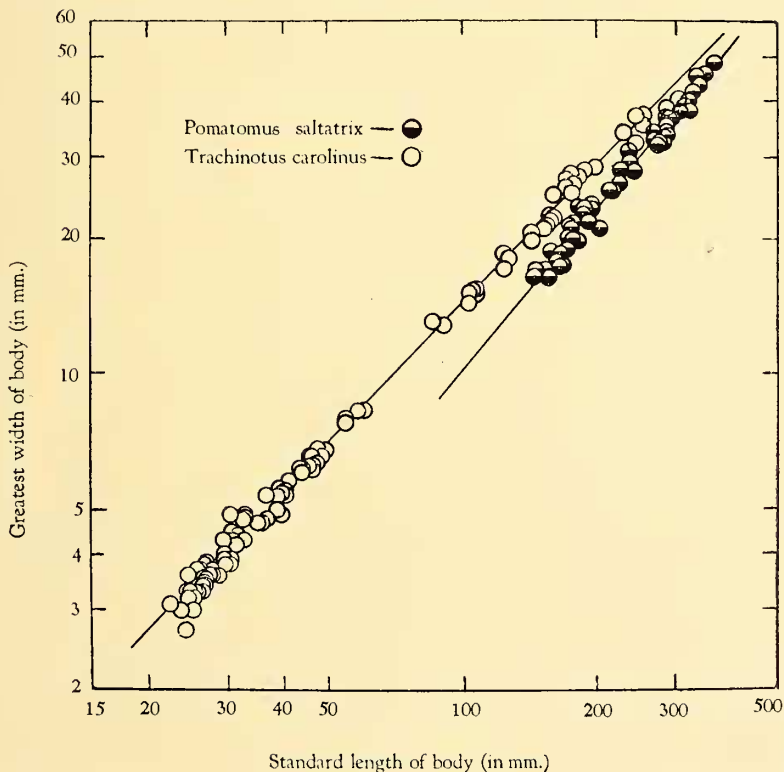
TEXT-FIG. 10. Greatest width of body relative to the standard body length; logarithmic plotting both ways.
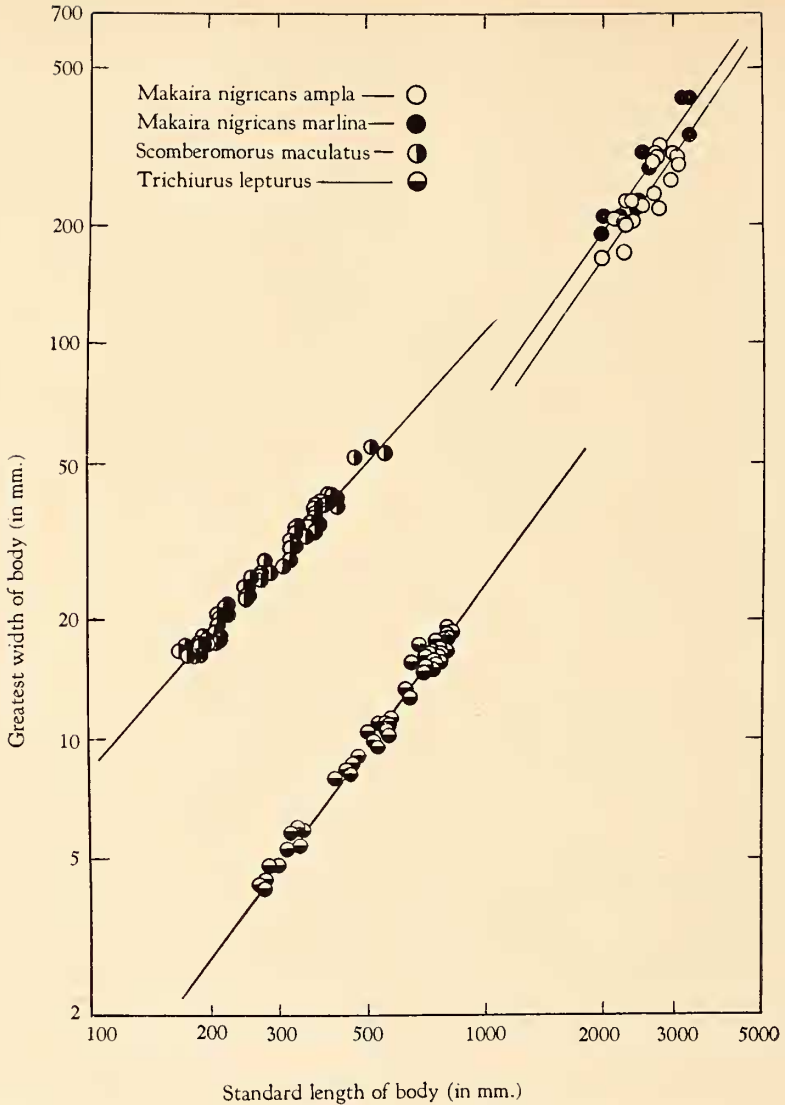
TEXT-FIG. 11. Increase of greatest width of body with increase of standard length; both variables plotted on a logarithmic scale.

the elongate forms. The gradient (k) for width increases as does that for depth, but in the sequence to the specialized mackerel-like types, the increase for the depth is slightly greater than that for the width. For the Carangidae this tendency is even more marked and results in a complete reversal of the intensity of growth in the transverse and vertical dimensions. Per unit increase the width shows greater growth than the depth in *Vomer setapinnis* and there is a general trend in the direction of *Trachinotus carolinus* where the depth now maintains greater increase than the width. These are broad tendencies, as shown here,

and it should be emphasized that for a more exact phylogenetic scheme, where generic and specific tendencies may be followed, more complete data are necessary.

There is a pattern of growth that is individual for each species but each pattern conforms, nevertheless, to a general scheme indicative of the trends of the larger groups. This seriation of the gradients of growth for the species suggests that phyletic lines can be determined by the allometric method and that change in the growth gradients is the mechanism by which the course of evolution proceeds. If so, the mathematical analysis of the interspecific changes in the
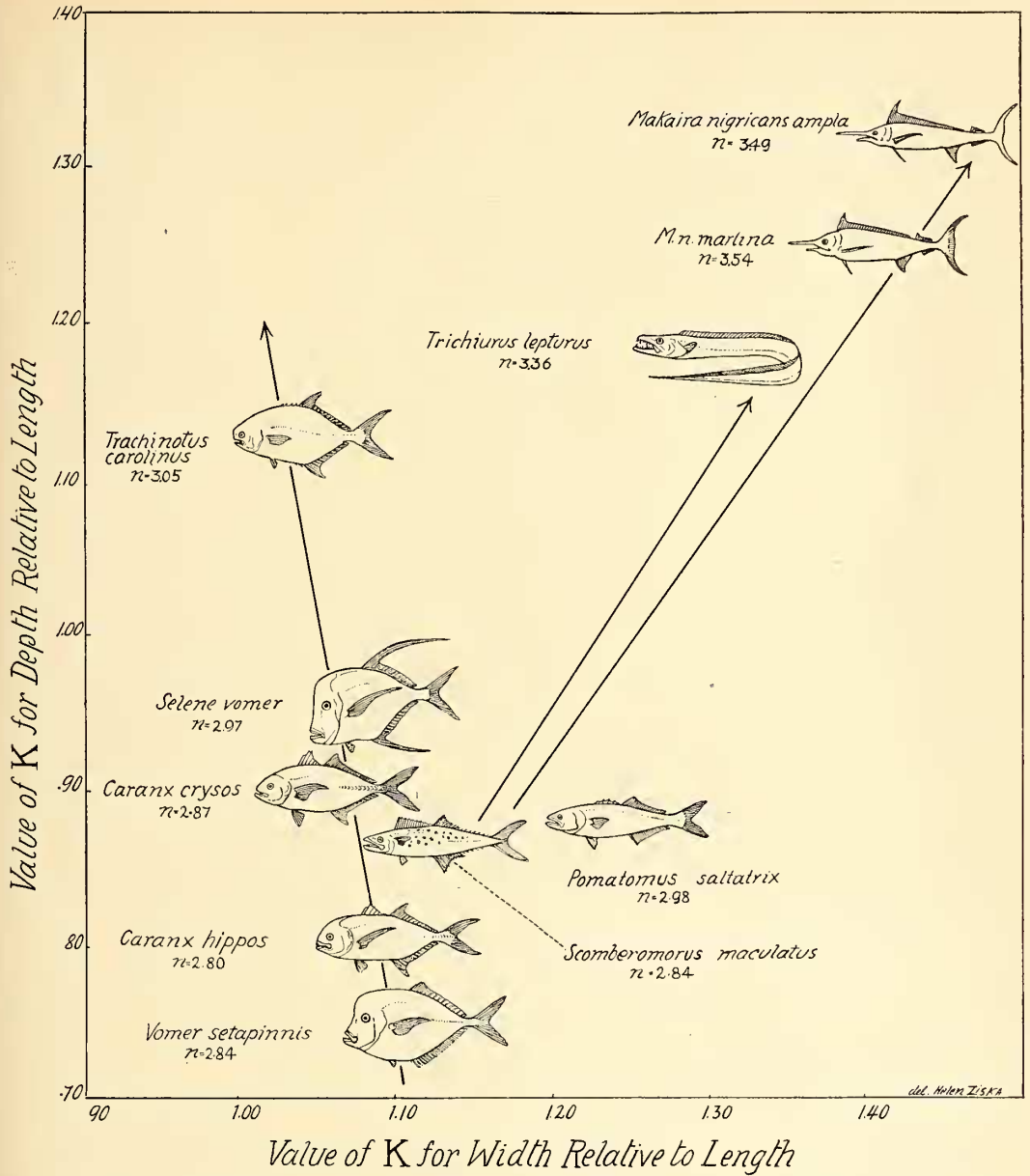
TEXT-FIG. 12. The various species of the Scombroidei plotted according to the values of *k* for depth relative to length and width relative to length. Both ordinate and abscissa are for increasing units of *k*. The value for the increase of weight relative to the length (*n*) is given for each species.

proportions and form of the organism should be a further tool to the phylogenist and systematist.

The divergence of the gradients for the Carangidae on the one side and the Scombridae and immediate allies on the other (Text-fig. 12) is in harmony with the view that these gradients reflect phylogeny. The sepa-ration of lines for the carangids and scom-broids indicate broadly the phylogenetic division accepted by many workers, either as separate lines within the Scombroidei or as independent modifications of a typical percomorph (serranid) stock. The Carangi-dae are grouped with the Scombridae and related families into a single suborder, the

Scombroidei, by many authorities, including Jordan and Evermann (1896, p. 862), Starks (1909, 1910) and Gregory (1933, p. 300). In their view the carangids, although possessing many percoid characters, appear to be even more closely related to the true scombroid families and can therefore be bracketed into a percomorph suborder, the Scombroidei. Tate Regan (1909, 1929, p. 321), however, refers the carangids to the percoid suborder and the true scombriforms to a separate suborder, the Scombroidei.

The primary fusiform body, illustrated by the mackerels, is a specialized stage away from the general, although somewhat deep-bodied, percomorph types. *Scomberomorus maculatus* has the initial growth index characteristic for the fusiform body ($a = 0.0000288$). This mackerel, however, maintains the early fusiform condition as it grows (k for depth = 0.87, Table 2). The most advanced stage away from the primary fusiform body is the elongate type represented by *Trichiurus lepturus*. The fusiform condition has been lost by excessive elongation ($a=0.0000000674$). *Makaira* may be classified as a specialized fusiform type. The initial growth index is very low ($a = 0.000000161$ for *M. n. ampla* and 0.000000118 for *M. n. marlina*) and like *Trichiurus* they are very slender fish early in development. They attain their fusiform condition only through the intense gradients at work during their growth.

There is no evidence of any Scombridae appearing until the Eocene, when they are already fusiform, primarily elongated forms with a vertebral number of 30-50. In this group total length has increased due to the increased number of vertebrae (the primitive acanthopterygian number is 10 + 14). The increase in vertebral number would seem to be a normal method of assuming the fusiform condition early in ontogenetic growth and maintaining it throughout life, providing there was no excessive increase in depth. The geological evidence would place the mackerel group as an early (Eocene) offshoot of its percomorph ancestor.

The mackerels illustrate the first step toward the elongated form represented by the Trichiuridae. The independent trichiurid line begins with *Ruvettus*, which is close to the mackerel type, and follow through by successive stages in modification and elongation until the end stage represented by *Trichiurus* is reached. *Trichiurus* is secondarily elongated (its vertebral number is 159).

The marlins, with 12+12 or 12+13 vertebrae, are already specialized with respect to this deviation from the basic percomorph pattern of 10+14. Early in their post-metamorphic development they are extremely long-bodied as indicated by their initial growth index. These fish lose their early

slenderness and attain a thick-fusiform streamlined condition, during their growth, through the maintenance of steep gradients; that is, through increase in the gross size of their parts. Thus the Istiophoridae present a distinct line of specialization resembling that of the Scombridae, in that both have a fusiform body—attained in the marlins during ontogenetic growth but present, however, at the beginning of and maintained during post-metamorphic growth in the mackerels. We are dealing with two widely divergent lines of evolution, each with striking differences (in vertebral number and growth constants) but nevertheless with considerable anatomical evidence to indicate a common heritage.

The bluefish (*Pomatomus*) has been considered the connecting link between the Serranidae and the Carangidae (Tate Regan, 1909), because of the intermediate character of its skull, general body form, caudal peduncle and caudal fin. In its external body form, however, it seems to have assumed the specialized contours of the fusiform mackerels, with which other authors have classified the genus. Its vertebral number still remains the primitive 10+14 percomorph number, but its form of body appears to be a case of parallel development of the fusiform type of body correlated with a predatory habit. The change has not been incurred in the mackerel manner, by an increase in vertebral number, but rather as in *Trachinotus* by a modification in relative growth (the initial growth index = 0.0000229 for *Pomatomus*). Since deepening of the body does not take place during growth as it does in *Trachinotus* (k for depth = 0.88 rather than 1.13, Table 2), the fusiform external mackerel condition established in the young stages of growth is maintained. *Pomatomus* could have well arisen from a serranid ancestor independently from the carangids—but perhaps from the same basic stock.

The relative growth method does not indicate the direction of phyletic lines and thus creates some difficulty in interpreting the line of carangid evolution. Since the increasing specialization of the scombroids appears to follow the line of divergence as indicated by the allometric growth method (see Text-fig. 12), such a trend may also be characteristic of the carangids. The value for the initial growth index is high for the deep-bodied *Selene vomer* ($a = 0.0000483$) and *Vomer setapinnis* ($a = 0.0000648$) but these fish become slenderer as they grow in size. *Caranx hippos* and *C. crysos* show the same relations for their post-metamorphic development. These fish can be designated primary deep-bodied types, regardless of whether the deep body of the early stages recapitulates the deep body of extinct ancestors or is a juvenile adaptation. *Trachino-*

tus carolinus shows a distinctly opposite trend. It is slenderer and more fusiform in the early stages of growth ($a = 0.0000264$) but becomes deepened during growth (k for depth is 1.13). It can thus be designated a secondarily deepened type.

Apparently two interpretations of this evidence are possible. These differences in the growth relations might well serve as evidence either that *Trachinotus* has been independently derived from the typical carangid line, or, as Gregory (1933) maintains, it is a longer-bodied derivative of the more primitive deep-bodied compressed types. The seriation as seen in Text-fig. 12 would seem to favor the interpretation that *Trachinotus* is a more specialized carangid in the direct line of ascent from the deep-bodied *Selene, Vomer* and *Caranx*. The initial growth index for *Trachinotus* is similar to that for the specialized *Scomberomorus* (Table 1). *Trachinotus* is only fusiform early in its post-metamorphic growth, but reverts to a deep-bodied condition during its ontogenetic growth. The Scombridae by increasing the number of vertebrae, have taken what seems to be a more normal and advanced method of assuming the fusiform condition. Thus their manner of attaining the fusiform condition was a more complete break from their ancestral type than *Trachinotus* was able to accomplish from the typically deep-bodied carangids or deep-bodied carangid ancestors, if it has come off independently from the carangid ancestors.

SUMMARY.

Relative growth methods are used to determine the relation between weight and body form in several fishes generally classed in the suborder Scombroidei.

The cube relationship between weight and length is only an approximation and in most of the species analyzed is not even closely realized. An allometric increase or decrease of weight in relation to length is correlated with the fact that the dimensions of the body are not necessarily a linear function of length. This non-linear relation may hold even when an isometric weight—cube-length condition is realized, for the changes in different dimensions may be compensatory.

Fish that attain a greater total size show a smaller bulkiness (initial growth index) early in their post-metamorphic growth, whereas the deep-bodied shortened fish have greater relative bulk at this stage of their growth. However, fish that are slim early in ontogenetic development tend to possess a high positive allometric distribution of weight during growth, and *vice versa*. This inverse relationship of the initial growth index to the growth constant is exponential and may be of some value in determining phylogenetic trends.

The depth in some species shows positive allometry, in others it is negative. All species studied, however, show positive allometry for the relationship of width to length. It is thus indicated that fishes which become relatively lighter during growth can do so only through a relative decrease in depth.

The differential growth in width proceeds more rapidly than the growth in depth in all the species with the execption of *Trachinotus carolinus*, where this condition is reversed. Thus, in the majority of scombriform fishes studied, the change to a larger fish proceeds more rapidly along the transverse than along the vertical axis.

In general there is a negative correlation between the values of the initial growth index and the values of the growth constants for the dimensional proportions. Species that are deeper or wider initially become relatively slenderer or thinner with age, and *vice versa*.

Closely allied members of the various families have similar coefficients of growth partition, but specific differences are nevertheless maintained.

The interspecific trends of the ontogenetic growth constants suggests the possibility that phyletic lines can be determined by the allometric method. The pattern of growth that is individual for each species seems to conform to a general scheme indicative of the evolutionary trends of the larger groups. Differences in relative growth trends within the Scombroidei of earlier authors characterize separate groups that have been or might be regarded as representing either separate divisions within the Scombroidei or entirely independent parallel phyletic lines.

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